Caldasia 26(1) 2004: 125-150

PHENOLOGICAL PATTERNS OF WOODY VEGETATION AT TINIGUA PARK, COLOMBIA: METHODOLOGICAL COMPARISONS WITH EMPHASIS ON FRUIT PRODUCTION

Patrones fenológicos de vegetación leñosa en el Parque Tinigua, Colombia: comparaciones metodológicas con énfasis en la producción de frutos

Pablo R. Stevenson
DPAS, SUNY at Stony Brook, New York. Departamento de Ciencias Biológicas, Universidad de Los Andes. Bogotá, Colombia. pstevens@uniandes.edu.co

ABSTRACT

Phenological patterns have a great influence on community ecology. I have quantified fruit abundance using fruit traps, phenological transects, and observations on marked trees of selected species. All methods showed the main peaks of fleshy fruit production between the dry period and the middle of the rainy season. Wind, water, and mechanically dispersed seeds showed a peak of production at the dry period. According to the number of individuals on transects, flower abundance showed predominantly two peaks, one at the end of the rainy period and one in the dry period. This pattern was positively correlated with solar irradiance estimates and differences between maximum and minimum temperatures, which tend to occur on dry days when the activity and abundance of pollinating insects seemed to be high. There was also a good correlation between relative day length and the density of flowering individuals, which suggest that this variable could trigger flowering patterns. Although many species lose their leaves in the dry period, the production of new leaves does not seem to be associated with any particular season. I used a new method to quantify fruit production for each species (in kg/ha), based on phenological transects, corrected visual estimates, and dry fruit weights. The mature forest produced more fruits than the other forests, and the flooded forest showed less fruit production during the dry season and the beginning of the rainy period. In contrast, average density of fruiting trees was similar or slightly greater in the flooded forests than in terra-firme forests during the middle part of the rainy period. Finally, I estimated how long the transects should be in order to get adequate estimates of fruit production, and I found that in general at least 7 km are necessary to get good estimates for terra firme forests at Tinigua.

Key words. Flowering, fruiting, leafing, methodology, plant phenology, Tinigua Park.

RESUMEN

Los patrones fenológicos de las plantas tienen gran influencia en la ecología de comunidades. He cuantificado patrones fenológicos usando trampas, transectos, y observaciones de individuos marcados. La mayor producción de frutos carnosos ocurre entre la época seca y la mitad del período lluvioso. Las semillas dispersadas por viento, agua o mecánicamente mostraron picos de producción en la estación seca. La producción de flores suele mostrar dos picos, uno al final del período lluvioso y otro en la estación seca. Estos picos están correlacionados con estimativos de radiación solar y con las diferencias diarias de temperatura, que tienden a ocurrir en días secos cuando la actividad y abundancia de insectos polinizadores es mayor. Hay una buena correlación entre la longitud relativa del día y la densidad de plantas con flor, lo que sugiere que esta variable puede ser el agente que dispara la floración en muchas especies. Aunque muchas especies pierden sus hojas en el período seco, no se encontró un patrón estacional en la producción de hojas jóvenes. Utilicé un nuevo método para cuantificar la producción de frutos, basado en transectos, estimativos visuales corregidos y el peso seco de los frutos. El bosque maduro produjo más fruta que otros tipos de bosque, y el bosque del plano de inundación mostró menor producción en la época seca y el comienzo de la lluviosa. En contraste, la densidad media de plantas fructificadas fue similar o ligeramente mayor en los bosques inundables que en los de tierra firme hacia la mitad del período lluvioso. Finalmente, estimé que tan largos deben ser los transectos para obtener una muestra adecuada de producción de frutos, y encontré en general que son necesarios al menos 7 km para los bosques de tierra firme del Parque Tinigua.

Palabras clave. Fenología, métodos fenológicos, Parque Tinigua (Colombia), abundancia de flores, frutos y hojas.

INTRODUCTION

Plant phenological patterns vary in time and space, and particularly fruit and seed abundance may show large variations (e.g. Herrera 1998). Climatic and biotic factors that might trigger and impose selective pressures on phenological phases are still a matter of discussion (Corlett & LaFrankie 1998, Curran & Leighton 2000, Sakai *et al.* 1999, Wich & Van Schaik 2000, Wright 1994, Wright 1995). Although it is difficult to control these factors experimentally (e.g. climate), especially at large spatial scales, it has been possible to modify some of them to test predictions about the importance of different factors on phenological patterns (e.g. water augmentation as in Augspurger 1982, Wright 1991). Phenological patterns have wide ecological implications on the responses of the animals that feed on plants and, therefore, are the focus of many ecological studies. Fruit abundance is usually an important parameter associated with the behavior of frugivores (Fuentes 1992, Hill & Agetsuma 1995, Koenig 1997, Loiselle & Blake 1991, Overdorff 1993, Peres 1994b, Terborgh 1983, Tutin *et al.* 1997, van Schaik *et al.* 1993, Curran & Leighton 2000, Kaplin *et al.* 1998, Knott 1998, Mandujano 1999, Renton 2001, Stevenson *et al.* 2000a, Wrangham *et al.* 1998, Wright *et al.* 1999). For example, at least one diet category was highly correlated with estimates of ripe fruit abundance in four primate species studied at Tinigua (Stevenson *et al.* 2000a), suggesting that their diets depend on fruit production patterns.

The relevance of phenological studies and the need for gathering comparative information on theses topics have promoted research on methodologies for describing and measuring phenological patterns (Chapman *et al.* 1992, Chapman *et al.* 1994, Hemingway & Overdorff 1999, Newstrom *et al.* 1994, Stevenson *et al.* 1998, Zhang & Wang 1995). For example, fruit abundance has been quantified using fruit traps, phenological transects, and area-based samples (Blake *et al.* 1990). Fruit traps allow to obtain quantitative information on fruit production in standard units (i.e. mass.area^{-1}.time^{-1}). However, it measures a residual quantity that is not consumed by frugivores (Terborgh 1983).

In some cases, it is possible to estimate the actual number of fruits that could have fallen in the traps, when other fruit parts or receptacles that are not consumed by the frugivores also fall into the traps (e.g. Stevenson 2002). However, this method is also highly dependent on trap location (Stevenson *et al.* 1998) and therefore, a large number of traps is needed to detect species-specific patterns of production, especially in diverse communities. Furthermore, trap design may affect results, particularly when fruit removal from traps is not prevented (Kollmann & Goetze 1998, Zhang & Wang 1995), and trap monitoring is usually more time consuming than alternative methods, especially if results are presented in terms of dry mass. Based on the reasons already mentioned, in former studies, we have recommended the use of phenological transects to assess relative fruit abundance (Stevenson *et al.* 1998).

The method of phenological transects has been considered to be adequate for detecting production even of scarce species, which other methods are unable to detect (Hemingway & Overdorff 1999). This method can also give quantitative information if relative production of individual fruiting trees can be estimated (Janson & Chapman 1999). Fruit production obtained through the transect method can be estimated based on visual quantification of fruits on the trees, on tree measurements such as diameter at breast height (DBH) and/or crown volume. These estimates have been reported to be correlated with fruit production of some plant species (Chapman *et al.* 1992, Hubbell 1980, Leighton & Leighton 1982). Direct counts are known to be an efficient method to quantify crops of large-fruited species. However, large inter-observer variation occurs when counting small fruits, as well as the probability of assigning inaccurate estimates increases (Chapman *et al.* 1992).

This manuscript has three specific objectives: 1) To show the general patterns of fruit, flower, and leaf production in a terra firme forest in Colombia, using different techniques, and to relate the patterns to climatic variables such as rainfall, temperature, and cloudiness. 2) To describe a new method to estimate fruit production based on phenological transects, and to compare this method to alternative ways for assessing fruit abundance. 3) Finally, based on an extensive sampling effort mode during the period of high fruit abundance to assess the sample size necessary for phenological transects. I addressed the following questions regarding this particular sampling unit: A) how much sampling effort will be needed to sample all fruiting species in the community? B) what minimum transect distance will be required to get a relatively constant estimate of fruit production in terms of the number of fruiting trees/km and the basal area of plants producing fruits?, and C) what is the minimum sampling effort to assess the relative contribution of the most important plant species producing fruit? In spite of the importance of fruit abundance estimates, very few studies have focused on the sampling effort necessary to get a consistent phenological pattern. The final part of this paper was intended to provide answers to that particular concern when considering a lowland forest and focusing on animal dispersed fruits, which have been strongly associated with community structure in Neotropical forests (e.g. Stevenson 2001).

METHODS

Study Area

This study took place in a tropical rain forest on the eastern border of Tinigua National Park west of La Macarena Mountains. The study site is located on the west margin of Río Duda (2º40´N, 74º10´W, 350-400 m elev.) at the CIEM (Centro de Investigaciones Ecológicas La Macarena), Departamento del Meta, western Amazonia, Colombia (Stevenson *et al.* 1994). The soils in the study area have different geological origins (Botero 1998). The flat forms along Duda River were formed very recently in the Holocene by the accumulation of sediments in the usual dynamics of white water meandering rivers (Terborgh 1983). These soils are richer in nutrients than in the non-flooded areas. The soils on the high terraces have a complex origin, with some components formed during the Tertiary period and others in the early Quaternary period (Botero 1998). These soils correspond mainly to Plio-Pleistocene alluvial soils that have been subject to recent tectonic fractures which have produced the differences in height between the river level and the hill crests of up to 65 m (Hirabucki 1990). These plates have been subject to erosion by water, forming meandering brooks and narrow canyons that are the cause of the undulating topography typical of the terra firme forests. These sedimentary soils were deposited mainly from periods of the latest Andean uplift, so that they are relatively young and more fertile than the typical soils in central Amazon basin (Botero 1998)

Five major forest types have been defined in the area within two major landscape units, the upland non-flooded forests and the forest on flood plains (Stevenson 2002). Non-flooded areas: 1). Mature forest, localized on hill ridges, with high and somehow continuous canopy and 2) open-degraded forest, localized on erosion fronts, small valleys and brooklets and characterized by a discontinuous canopy and a thick understory. Flood plains: 1) Riparian forest, which is located on recently formed beaches and dominated by *Tessaria integrifolia* (Asteraceae), *Cecropia membranacea* saplings and several graminoids. This forest type is known to change along a succession to constitute the other two plant communities. 2) Flooded forest on raised bars, which flood only on occasional years. This type is dominated by *Guarea guidonia* and *Cecropia membranacea* trees, and the understory includes a variety of plants including species of the mature forests and large herbs such *as Heliconia episcopalis*. 3) Flooded forest on low basins, on low-lying areas subject to annual flooding. The trees *Laetia corymbulosa* and *Luehea cf. tessmannii* dominate the tree community, and *Heliconia marginata* dominates the understory.

Rainfall is seasonal in the region, with a 2-3 month dry period occurring between December and March. Average annual precipitation at Paujil during the three study years when the density data was taken was 2782 mm. Mean climatic records are shown in Fig. 1.

Phenological Methods

Phenological transects

We censused a total of 5598 m of transects twice a month during three yearly cycles (April 1990 – March 1991, August 1996 – July 1997, and February 2000 – January 2001). We identified all woody plants (trees, treelets, and lianas) bearing ripe endozoochoric fruits in the transect and we measured the DBH of each (> 5cm) projecting its fruiting crown above the twelve phenological transects (about 450 m each), which were located along trails. Transects were located in the three main forest types (mature, open-degraded, and flooded forests) and in similar proportion of their abundance (6, 4 and 2 transects respectively). We used the number of fruiting plants and the basal area of trees as measures of fruit abundance. Basal area has been used to estimate of fruit abundance because it has been shown that large trees produce more fruit than small ones (Chapman *et al.* 1992). Therefore, fruit production was assumed to be proportional to the basal area of fruiting trees in transects. Since most individual plants bore fruit for more than one consecutive biweekly period, its production was divided among all sampling episodes when the plant had ripe fruits, and the division was not homogeneous because fruit production tends to peak at the middle of the crop duration. We calculated community-wide fruit production for each period as the sum of the fraction of the basal areas of all the trees fruiting during that period, assuming a triangular fruit production pattern for each tree (see Stevenson *et al.* 1994), where fruit production of each plant was assumed to increase linearly until the midpoint of the crop duration and then decrease linearly in a symmetrical fashion, and the maximum production (the height of the triangle) was kept constant at the same scale as one biweekly period unit. Lianas were not included in the analysis using basal area, but were included to estimate the density of fruiting plants.

For the second and third years, I also estimated the number of individuals bearing wind, water, and mechanically dispersed fruits and seeds on the transects, as well as the number of plants with open flowers (including trees with DBH>5cm and vines with DBH>2cm). In some cases, for example for vines, it was difficult to distinguish the seed shadows originated from closely located individuals of the same species. Thus we assumed that shadows separated less than 10 m apart belonged to the same individual.

Fruit traps

We distributed a total of 300 fruit traps (800 cm² each) in three forest types in a similar proportion to the area covered by each forest (150 traps in mature forest, 100 in open-degraded forest and 50 in flooded forest)(Stevenson *et al.* 1994, Stevenson *et al.* 1998). We placed 25 traps in each of the 12 transects established for phenological observations. Each trap location within a transect was determined by three random numbers, as 1) the spacing between adjacent traps (10-20 m), 2) the side of the trail (right or left), and 3) the distance to the trail (0-10m). Trap contents were collected biweekly during one year cycle (April 1990 – March 1991) and dried. Fruits and seeds were identified at the species level according to the fruit guide of the study area (Stevenson *et al.* 2000). Here I report only on production of ripe fruits for comparative purposes with phenological transects.

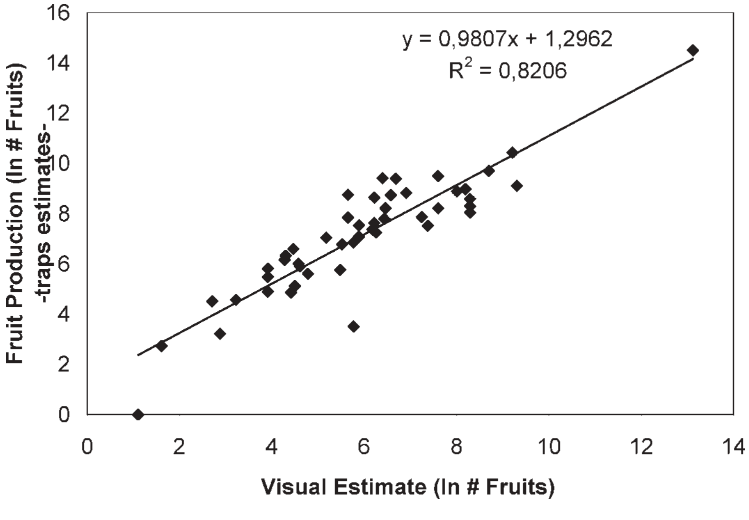

Figure 1. Annual variation in rainfall, mean temperature, and irradiance (as a 0-5 index) from three years of data collected at Puerto Paujil Station in Tinigua National Park.

Phenology of Selected Species

We monitored phenology of six individuals of 24 species that are either common in the area or have important ecological roles in the community (Stevenson, Quiñones & Ahumada unpublished), because their fruits were known to be consumed by a variety of animal species. We recorded the presence of ripe and unripe fruits, flowers, and leaf status at biweekly periods during one year (March 1990-1991). We included species in the three different forest types.

A New Methodology

Based on the information obtained from the phenological transects, combined with fruit counts on individual plants, estimates of the effective area sampled, and models of fruiting distribution through time for each plant, I calculated estimates of fruit production during the last study period (Feb/00-Jan/01). The basic information from the original phenological transects was the number of individuals bearing ripe fruits. Additionally, we visually estimated the number of fruits in the trees, treelets, and lianas at the beginning of the fruiting season, either by counting all fruits in the plants or, when crop size was high (>50), by extrapolating from the number of fruits counted in a few branches. In those cases when we detected fruit production after frugivore activity had started, we also estimated the number of fruits on the ground and added it to the number of fruits counted at tree crown. The visual estimation method is known to be inaccurate, especially for large crops of small sized fruits (Chapman *et al.* 1992), and that was the case in our approximations. However, we corrected our estimates based on a set of 10 plant species which fruit crop was calculated as well by fruit traps (usually six trees for each species, Stevenson 2002). A log-log linear relationship allowed us to correct our estimates (Eq.1):

Ln (Number of Fruits) = 1.2962 + 0.9807 * Ln (visual estimate) Eq. (1)

Using equation (1) I was able to predict 82% of the variation in fruit production estimated from traps for that set of species (Fig. 2). Other approximations to estimate fruit production such as crown area of fruiting trees were less correlated with the fruit trap values than the visual estimates (r^2= 0.32). Thus, in spite of

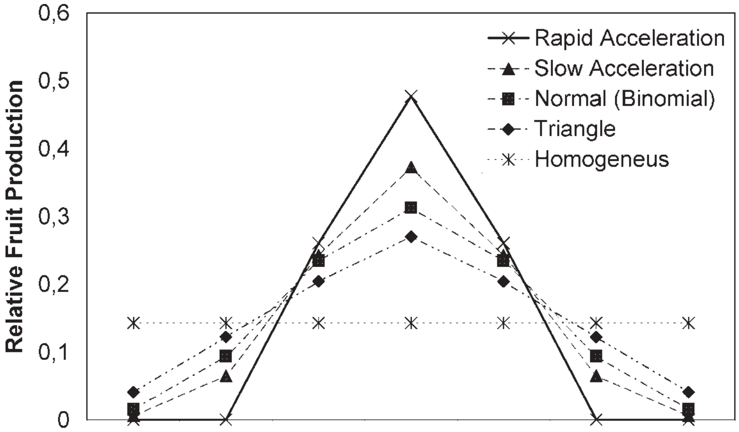

Figure 2. Relationship between visual estimates of fruit production and estimates from fruit traps, for 10 plant species at Tinigua National Park.

the relative inaccuracy of the visual estimating method, we could correct our visual estimates for almost all plant species when using equation 1. The correction was not applied to the cauliflorous species of the study site (*Theobroma cacao* L, *T. glaucum* H. Karst, *Couroupita guianensis* Aubl., *Grias peruviana* Miers., and *Leonia crassa* J.B Sm. & A. Fernández), because they have large fruits that are not covered by leaves, therefore the original estimates were probably not biased.

Then I transformed the corrected number of fruits to fruit mass, using the average fruit weight of each of the 182 fruiting species found in the transects. I usually estimated dry weight for an average of six fruits (60% of the species) or from a single medium ripe fruit from a collection of fruits (40%). The procedure of using small sample sizes is unlikely to greatly affect the final result of the analyses, because in general there is low variation of morphological variables within species. The fruit mass of each tree was expressed in terms of biomass production (Kg/ha) by estimating the effective sampled area. This area varied among species, because we were more likely to notice on the transects fruits from a large tree than from a small one. Thus, the effective sampling area was larger for large trees species. This area was calculated as the product between the total transect length (5598 m) and the effective transect width for a given species. The latter was calculated as the average perpendicular distance between the transect and the tree trunk (Burnham *et al.* 1980), taking into account the relationship between tree size and detection distance. What I did was to find a relationship between DBH (as a surrogate of plant size) and perpendicular distance between the transect and the tree trunk, that was measured in the field for each fruiting tree. To estimate the effective transect width for a plant of a given size, I used two regression lines (Eq. 2 and 3): one for trees producing fruits in the plant crown and the second for palms and cauliflorous trees. Two distinct equations were used because there is a higher probability to find fruits on the ground from a fruiting tree than from a similar-sized fruiting palm or a tree producing fruits on the trunk. Both lines have the same slope as in the relationship between DBH and distance (both log transformed), and the intercept was the average between the intercept in the original regression line between DBH and distance, and the intercept of the line with the same slope, but crossing by the more distant plant in the analysis.

$\mathrm{Ln}\,(\mathrm{Transect\ Width} + 1) = 0.248 + 0.184 * (\mathrm{Ln\ DBH})$ Eq. (2)

$\mathrm{Ln}\,(\mathrm{Transect\ Width} + 1) = 0.240 + 0.273 * (\mathrm{Ln\ DBH})$ Eq. (3)

Both equations showed significant positive slopes ($F=6.0$, $p=0.02$, $r^2=0.03$, $n=210$ plants and $F=91.6$, $p<0.0001$, $r^2=0.10$, $n=806$; respectively), however, the regression coefficients were low because large plants can be detected at large and small distance from the transect. Transect width was about 9 m at each side of the trail for the largest trees and about 5 m for the largest palm. In absence of good physiognomic data for relating DBH and crown volume of lianas and hemi-epiphytes, I assumed a constant transect width for those species, which was the average for all other plant species (4.1m).

Finally, I distributed the fruit crop production of each individual recorded in transects during the periods when they were bearing ripe fruits. Two production patterns were assumed, a homogeneous distribution and a discrete approach to the normal distribution. These two patterns were based on empirical measurements from trees with fruit traps, and from biweekly recordings on the percentage of the total fruit crop available. A homogeneous distribution was found for a subset of species to which it was not possible to detect any particular peak in fruit production while fruiting (Table 1). Thus total crop size of those species was divided equally among the periods when the plant was producing ripe fruits. For the remaining species there was a consistent tendency to produce more fruits in the middle of the ripening period. Among 5 different models, the best fit for 25 trees of different species was for a discrete approximation to the normal distribution (using the coefficients for the binomial distribution: r=0.81). For example, for a crop lasting 7 biweekly periods I used the following coefficients to multiply the total fruit crop for that tree: 1/64, 6/64, 15/64, 20/64, 15/64, 6/64 and 1/64. The coefficients (1, 6, 15, 20, etc.) can be easily obtained from a Pascal triangle, in the row of seven columns. The results of the new methodology are expressed as the total contribution of each species in a particular phenological sampling period. It was calculated by summing the relative contribution (given the temporal distribution explained above) of every individual of that species producing fruits in such period.

Table 1. Plant species with relative homogeneous fruit production during their fruiting episodes at Tinigua Park.

Bursera inversa	(Burseraceae)
Cecropia sciadophylla	
Cecropia engleriana	(Urticaceae)
Cecropia membranacea	
Couroupita guianensis	(Lecythidaceae)
Grias peruviana	(Lecythidaceae)
Guarea guidonia	(Meliaceae)
Oenocarpus bataua	(Arecaceae)
Protium aracouchini	(Bureseraceae)
Tournefortia foetidissima	(Boraginaceae)

Intensive Effort to Assess Sampling Size for Phenological Transects

In May 2000, during the period of highest fruit production in the study site I carried out a total of 34 phenological transects along the main trails in the study area in two days. This large sample was used to estimate the sampling effort needed to reach stable values for some variables used to describe fruit production. Each phenological transect was 500 m long, so that total sampling distance was 17 km. I measured the DBH of all plants (> 5 cm) that projected their fruiting crowns above the transect as described in the phenological transects method. I used the number of fruiting species, the number of trees, and their basal area as measures of fruit abundance (Chapman *et al.* 1992, Leighton & Leighton 1982). I did not consider crop size, nor biomass because fruit counts were not available for most trees (especially those that started producing fruits before the survey). I located all transects in terra firme forest to avoid inclusion of other forest types, such as secondary and flooded forests, which have different plant communities (Stevenson *et al.* 1999, Stevenson 2002).

The total number of species, basal area and number of trees were plotted as a function of transect distance. Because these curves can vary depending on how transects are ordered for analyses, I used the average values of six simulations, in which the entrance order of each one of the 34 transects was set at random. For these analyses I estimated the 95% confidence limits from the variation in all the 34 independent transects. Then I imposed this range to the final estimate, to examine the distance where the values remained within these confidence limits.

For the analysis of relative representation of different species in the sample I used basal area estimates and an index based on ranks. I estimated the total basal area of each fruiting species at different sampling distance (1.5, 3, 5, 7, 9, 11, 13, and 15 km) and I obtained the average basal area from six simulations where the order of transects was set at random. I excluded lianas and hemi-epiphytes from this analysis because their basal area underestimates production. The following index was used to compare how the most important species varied as a function of sampling effort:

$\text{RSI}_{at} = \text{Ó}\,¦\,\text{rank i}_{a} - \text{rank i}_{t}¦/\,\text{N(N+1)}$

The rank similarity index (RSI) compares the rank of each species i between an intermediate sampling effort (at distance a) and the total distance t. The index is based on the absolute difference in the rank (in decreasing order) for each plant species i, comparing the final rank with the rank of that species at a particular sampling effort. I computed the index as the summation of those absolute differences between the rank for the 20 most dominant fruiting species in terms of their basal area. In order to standardize the index for any number of species, the summation is divided by [N(N+1)], which is the maximum potential difference in ranks (where N is the number of species included, 20 in this case). Thus the index varies between 1 and 0, where zero is an exact match of all rankings. I set confidence limits for the index from 5000 simulations, where I assigned a random rank (between 1 and 20) to the different species included in the top 20 list and then I calculated the index. I used this procedure to know the sampling effort necessary to find a relative contribution of different species similar in order to the contribution at the end of the sampling period (17 km, taking it as the best approximation of the true fruit abundance estimate).

RESULTS

General Phenological Patterns: Leaves and Flowers

Phenology of Selected Species. New leaves production did not show large variations during the year, but the proportion of leafless trees increased during the dry period (December to March) (Fig. 3). For that particular set of species we detected two peaks of flower production (Fig. 3), one at the end of the rainy season and the second during the dry period (February).

Phenological Transects. Regarding flowering, a very similar pattern was found from Aug/96 to Jul/97 in the three main forest types (Fig. 4. a. However, in the flooded forest the flowering peaks occurred about a month later and the peak at the end of the rainy period was less pronounced than in the terra

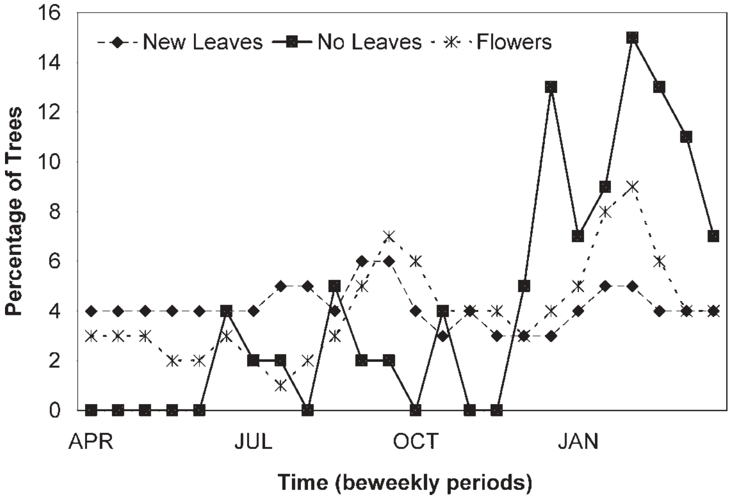

Figure 3. Patterns of flower and leaf production for a set of 24 tree species at Tinigua National Park. The percentage of individuals with no leaves, new leaves, and open flowers was calculated from biweekly revisions on six individuals for each species during one year (Apr/90-Mar/91).

firme forests. On the other hand, for the 2000, the flowering pattern at the community level was somehow different (Fig. 4.b) because the peak at the end of the rainy period was divided into two small peaks. The results of a multiple regression analysis to predict the number of plants with flowers in each biweekly phenological sample, indicated that only solar irradiation (positively) and relative day length (negatively) were correlated (F= 7.2, p=0.01, and F= 4.5, p=0.04, respectively). Although many other climatic variables were included (rainfall, mean, maximum, and minimum temperatures), the complete model explained only 41% of the variation in the number of flowering plants.

Fruit Production Patterns

Abundance of Abiotically Dispersed Fruits and Seeds. Abundance of fruits with wind, water or mechanical dispersed seeds was always high during the dry periods in every forest type (Fig. 5 and 6). There was a higher abundance of this kind of fruits during the rainy season in the flooded forest than in terra firme forests, and the pattern was very similar between two years, when the same

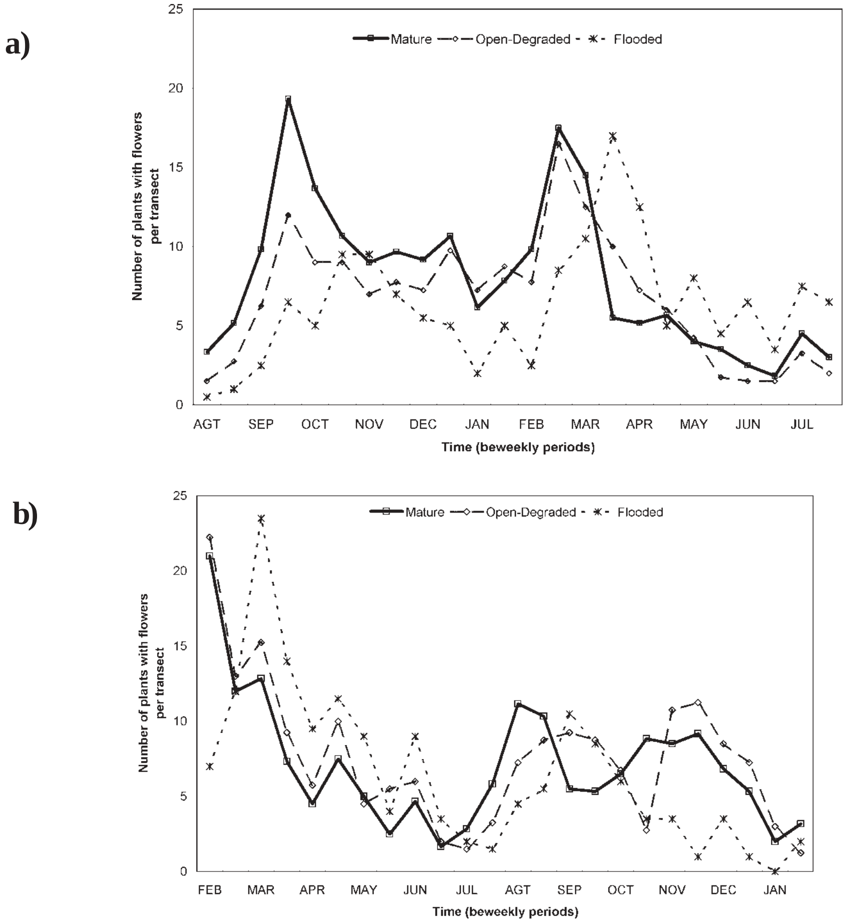

Figure 4. Patterns of flower production in three different forest types in Tinigua National Park, as the number of plants with flowers in the transects during two years. a). Ago/96-Jul/97. b) Feb/00-Jan/01.

phenological methodology was used (Fig. 6. a and b). A multiple regression analysis using the climatic variables showed that there is a high positive correlation between monthly solar irradiation and the production of this kind of fruits in phenological transects (F=22.0, p<0.001, df.=45). Irradiation was the only variable showing a significant partial regression coefficient and the overall model explained 60% of the variation of wind, water, and mechanically dispersed seeds abundance.

Abundance of Animal Dispersed Fruits. The pattern of animal dispersed fruits is different than abiotically dispersed seeds because the highest period of fruit abundance occurred at the beginning of the rainy period instead than in the dry period. This pattern has been very consistent among years (Fig. 7). The multiple regression analysis including all the climatic variables considered and four lag rainfall series showed that only rainfall and lag-rainfall showed significant partial coefficients. Restricting the analysis to these significant variables, a 2.5 months lag of rainfall showed the largest partial regression coefficient (rainfall: F= 27.3, r^2= 0.27; a month lag: F= 9.6, r^2= 0.29; and 2.5 month lag: F= 49.5, r^2= 0.39; all p< 0.001 comparison-wise). This model explained 69% of the variation in the number of fruiting plants in phenological transects.

The community pattern of ripe fruit production derived from different methods showed the same basic pattern (Fig. 8) and are positively inter-correlated (Table 2). The differences resulting from each method can be explained in part by methodological problems (see discussion section).

Table 2. Correlation coefficients between different methods to measure ripe fruit abundance at Tinigua during one year cycle (Apr/90-Mar/91)(from Stevenson *et al.* 1994).

	Fruit Traps	**Phenological Observations**	
	Production (Kg/ha)	Fruiting Trees (#)	Basal Area (dm^2/km)
Fruiting Trees	0.56		
Basal Area (dm^2/km)	0.57	0.70	
Marked Trees (#)	0.38	0.73	0.66

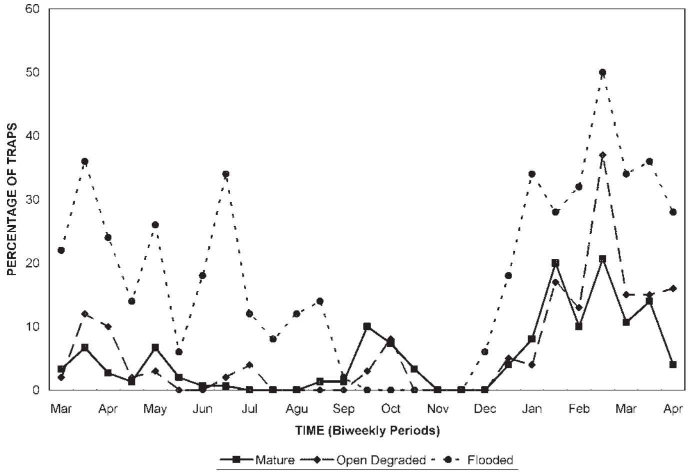

Figure 5. Patterns of wind, water and mechanically dispersed seeds abundance for three different forest types at Tinigua National Park (Apr/90-Mar/91), as the percentage of traps containing these kinds of fruits and seeds (Stevenson *et al.* 1998).

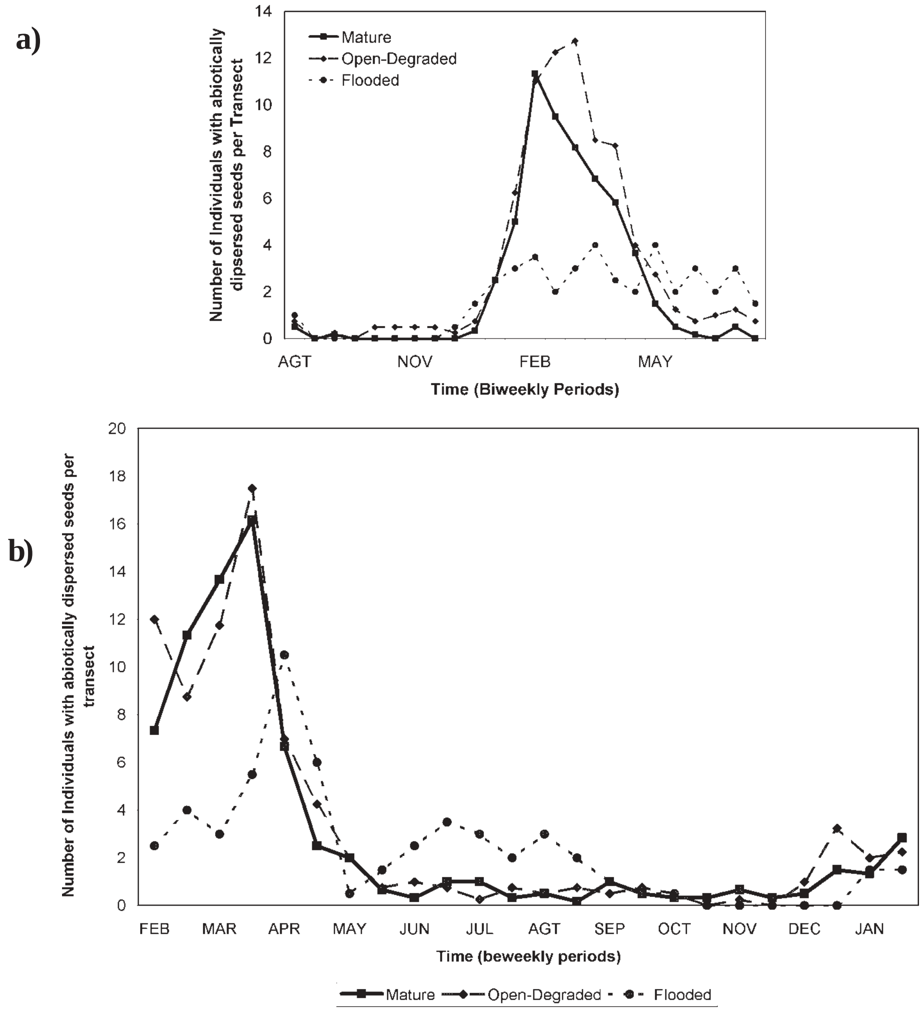

Figure 6. Patterns of wind, water and mechanically dispersed seeds abundance for three different forest types at Tinigua National Park, as the number of plants dropping fruits or seeds in the phenological transects in two different years. a). Ago/96-Jul/97. b) Feb/00-Jan/01.

Results from the New Method

The method used during the last study period showed the same basic pattern of fruit production (Fig. 9). There was an increase in fruit production (kg/ha) from the beginning of the dry period, highest peak occurred at the beginning of the rainy season, then production decreases in the middle of the year and the lowest production values happened at the end of the rainy period. I was able to reasonably estimate the production of each species through time, indicating that peaks are caused by the production of different species bearing fruits at the same time. Also few palm species (such as *Oenocarpus bataua* Mart. and *Astrocaryum chambira* Burret.) greatly contribute to the overall production.

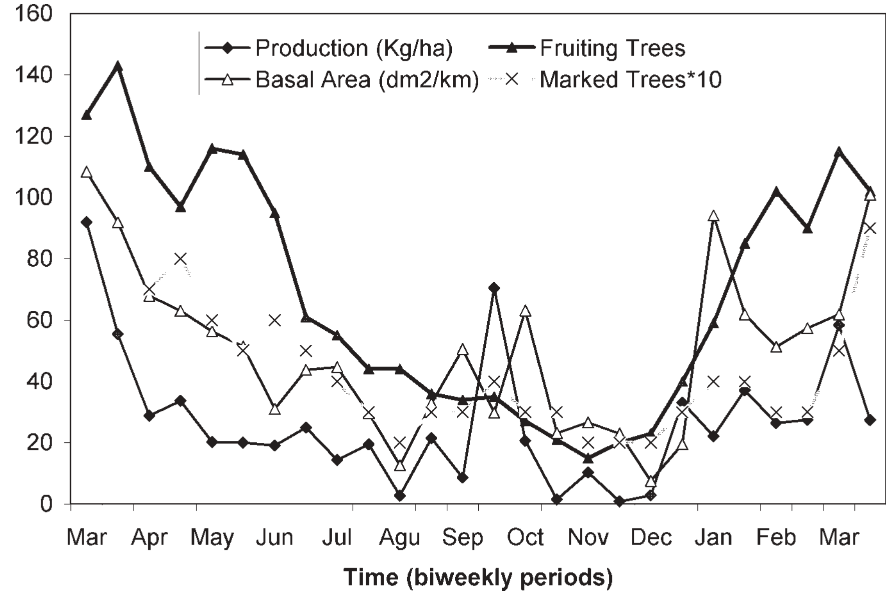

Figure 7. Inter-annual comparison of the pattern of fruit abundance regarding the number of plants registered with ripe fleshy fruits in 5.6 km of phenological transects at Tinigua National Park, during three-year cycles. Each line is not really continuous because the starting point in January was adjusted for comparative purposes.

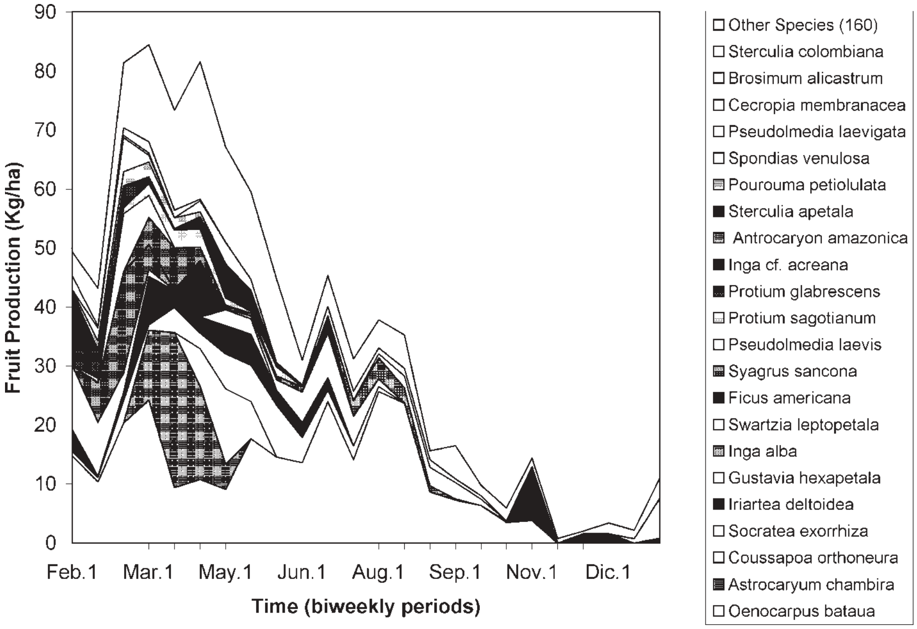

Figure 8. Comparison of four different approaches to quantify the temporal variation in fruit abundance at Tinigua National Park during a year cycle (Apr/90-Mar/91). Only ripe fleshy fruits were included for this analysis. Fruit production in this case refers to fruit trap estimates (based on Stevenson *et al.* 1998).

The new method quantified fruit abundance more precisely than other methods, such as those based on basal area or the number of individual plants in fruit (Table 3). For example, according to the basal area of fruiting trees *Oenocarpus bataua* is not included among the top ten species, while it is included when using other methods. The list based on basal area included many species characterized by very large trees that did not show necessarily a large production, at least during such year (e.g. *Brosimum alicastrum* Sw.).

In spite of the differences among methods regarding species-specific patterns of abundance, there was a similar community-wide fruiting pattern (Fig. 10). In particular, there was a very high correlation between the new method to measure fruit production and the number of fruiting trees in phenological transects (r^2=0.95). Basal area estimates were well correlated with the other methods as well (fruit production: r^2=0.77 and number of trees: r^2=0.80).

Between Year Variation

The general pattern of fruit abundance, regarding the number of fruiting trees on phenological transects, did not vary much between the three years when I have carried out phenological observations (Fig. 7). I found some variations in the amount of fruit produced by each species, and in few cases there was also temporal variation in the timing of production. However, those variations seem to be exceptions rather than the rule. For example, the total number of fruiting species found in the transects was similar (1990=157, 1996=191, and 2000: 177). Also about 70% of the species were shared between different years, and the most important species were fruiting have been recorded all years.

However, I have seen differences in crop size and duration between years. For example, the fruit production of *Inga cylindrica* (Vell.) Mart., an important plant species of the flooded for-

Table 3. Comparison among three different approaches to assess fruit abundance at Tinigua National Park. The table shows the 21 most important plant species producing ripe fleshy fruit during one year (Feb/00-Jan/01), and their relative importance according to each method.

Fruit Biomass (Kg/ha)		**Basal Area (cm^2)**		**No. Individuals**	
Oenocarpus bataua	262.1	*Gustavia hexapetala*	42850	*Theobroma cacao*	44
Astrocaryum chambira	58.5	*Brosimum alicastrum*	41822	*Protium sagotianum*	41
Coussapoa orthoneura	25.2	*Ficus andicola*	37393	*Gustavia hexapetala*	38
Socratea exorrhiza	43.4	*Ficus trigonata*	29642	*Protium robustum*	36
Iriartea deltoidea	40.6	*Ficus americana*	27614	*Socratea exorrhiza*	33
Gustavia hexapetala	37.3	*Apeiba aspera*	24715	*Pseudolmedia laevis*	32
Inga alba	28.2	*Pseudolmedia laevis*	24475	*Oenocarpus bataua*	32
Swartzia leptopetala	21.3	*Spondias venulosa*	24140	*Protium glabrescens*	32
Ficus americana	20.0	*Pseudolmedia laevigata*	22747	*Pseudolmedia laevigata*	30
Syagrus sancona	17.3	*Protium sagotianum*	22083	*Quararibea cf. wittii*	27
Pseudolmedia laevis	13.8	*Cecropia membranacea*	21021	*Crepidospermum rhoifolium*	16
Protium sagotianum	13.3	*Castilla ulei*	19657	*Iriartea deltoidea*	13
Protium glabrescens	12.8	*Inga cylindrica*	16933	*Cecropia membranacea*	12
Inga acreana	11.0	*Hymenaea oblongifolia*	15729	*Dendropanax caucanus*	12
Antrocaryon amazonica	10.9	*Oenocarpus bataua*	13897	*Apeiba aspera*	11
Sterculia apetala	9.9	*Neea laxa*	12970	*Protium aracouchini*	11
Pourouma petiolulata	9.7	*Couroupita guianensis*	12487	*Astrocaryum chambira*	10
Spondias venulosa	9.6	*Coussapoa orthoneura*	5885	*Oxandra mediocris*	10
Pseudolmedia laevigata	9.2	*Sterculia apetala*	9748	*Siparuna cuspidata*	10
Cecropia membranacea	8.4	*Ficus insipida*	9527	*Neea laxa*	9
Brosimum alicastrum	8.1	*Sapium laurifolium*	9465	*Euterpe precatoria*	9

est, was very low during the last sampled yearly cycle (2000), compared with other years. Also, as mentioned above, fig plants showed large variations within and also among years. In 2000, fruit production of *Gustavia hexapetala* (Aubl.) Sm. was delayed for about a month in comparison to other years. This difference explains the very low fruit production observed in December (Fig. 9), when fruit abundance usually starts to increase (Fig. 7).

Most of the species (with figs as the main exceptions) produce fruits once a year. Some years, I observed different fruiting episodes for individuals of other species such as *Brosimum* spp., *Pseudolmedia* spp., and *Clarisia racemosa* Ruiz & Pav. *Pourouma bicolor* Mart. usually produces one crop in the dry season and a second one in the middle of the rainy period, when fruit crops tend to be less productive.

Differences between Forest Types in Fruit Production

Fruit production during the dry season and the beginning of the rainy period is higher in the upland (Terra Firme) forests than in the flooded forests (Fig. 11). Density of fruiting sources tends to be on average higher in the flooded forests from the middle of the rainy season until the end of this period. However the variation is large enough so that the difference in density between flooded and Terra Firme forests is not statistically significant (see Fig. 11). Furthermore, looking at fruit mass estimates, mature forests usually showed the highest values compared to the other forests (Fig. 12). A similar result was obtained using fruit traps (Stevenson *et al.* 2000a).

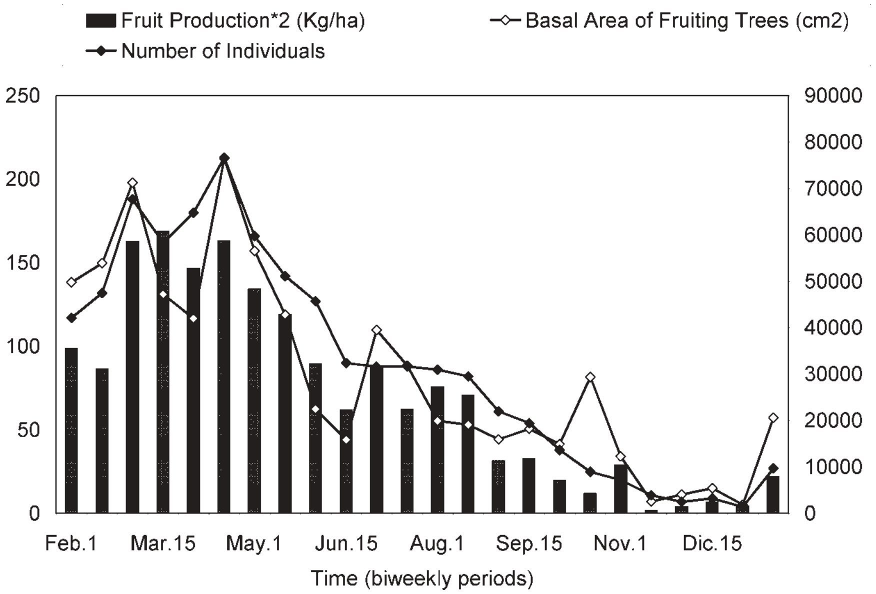

Figure 9. Temporal variation in ripe fleshy fruit biomass production in Tinigua National Park during one year (Feb/00-Jan/01), according to the new methodology presented in this study. Main species production is shown in different colors, and the upper line shows the overall production pattern. See text for methodological details.

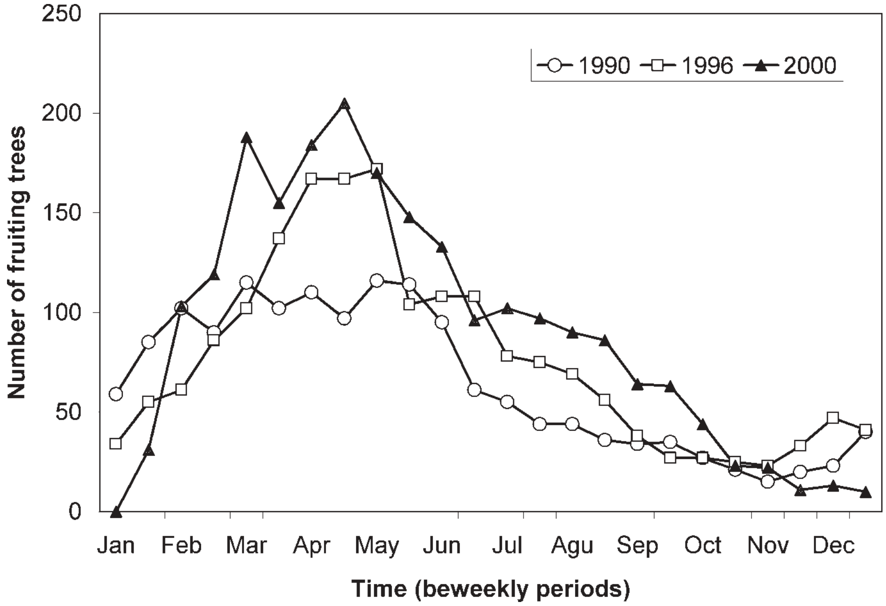

Figure 10. Comparison between the pattern of fruit production found using the new methodology and two approaches to assess fruit abundance: the number of fruiting plants in the phenological transects and the basal area of the trees found in the transects at Tinigua National Park for the last yearly cycle (Feb/00-Jan/01).

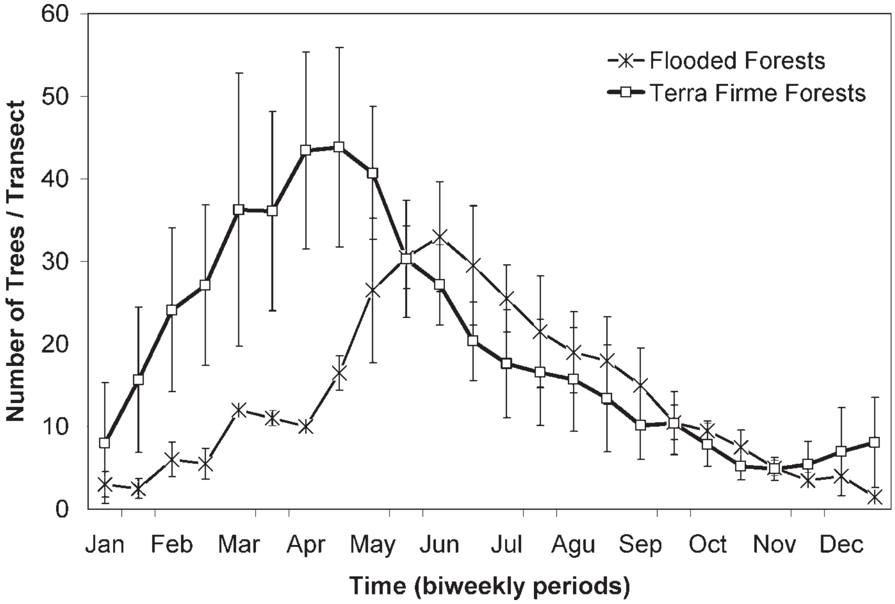

Figure 11. Seasonal differences in the density of ripe fleshy fruit resources in flooded and Terra Firme forests in Tinigua National Park. Bars represent the standard error from the number of individuals found in the phenological transects at each main forest type in three different years.

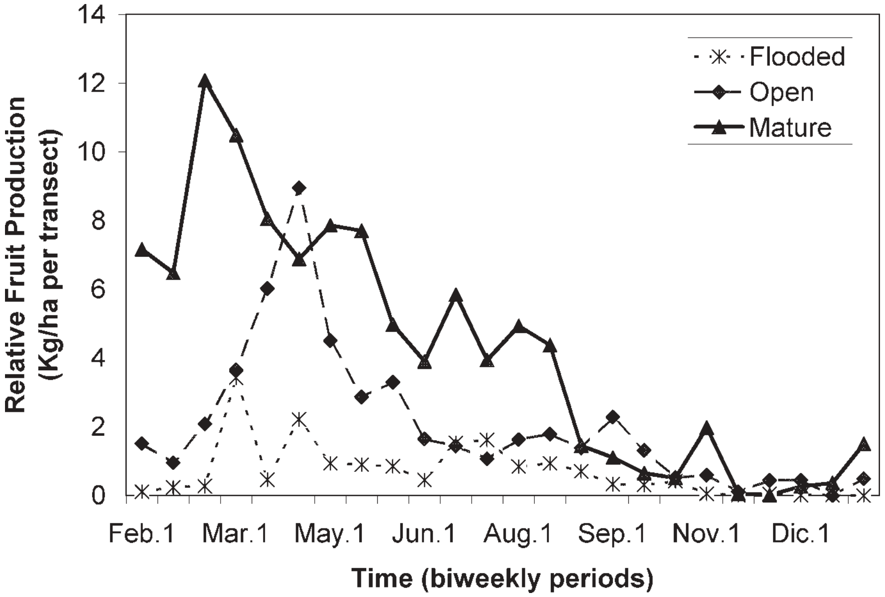

Figure 12. Comparison of fruit production patterns, using the new methodology, in the three different forest types at Tinigua National Park during one yearly cycle (Feb/00-Jan/01).

How long should the transects be?

I found 107 plant species producing ripe fleshy fruits in May 2000 in the 34 transects and after 17 km the accumulation curve does not reach a saturation point (Figure 13 a). In contrast the number of trees with ripe fruits*km^{-1} showed relatively stable values by the first three kilometers (Fig. 13 b). However, the 5% probability of finding a number of trees similar to the final estimate indicated that the estimate does not leave the confidence interval after the first 8 km. Although we found more variation above and below the final value of basal area of fruiting trees, the average value does not leave the 5% confidence limits after the first 10 km (Fig. 13 c).

The similarity rank analysis showed that the average index decreases as more transects are sampled and these indexes are included within the 5% confidence limits after the first 7-9 km (Fig. 13 d).

DISCUSSION

General Phenological Patterns

Phenological patterns at Tinigua National Park can be characterized by their temporal consistency, at least in the years when observations have been made. These patterns do not differ much from the results found in other Neotropical lowland forests with similar seasonal climate (Croat 1975, Daubenmire 1971, Frankie *et al.* 1974, Janzen 1967). Several hypotheses have used for explaining the advantage that plants might have when producing flowers in hot, dry periods, such as more visibility by pollinators in an leafless environment (Janzen 1967), and higher activity and abundance of pollinators. For example, bees seem to constitute the main pollinator guild in Amazonian forests (van Dulmen 2001), and they are more active in dry periods (Viana *et al.* 1997). Although our results did not provide support for any of these particular hypotheses, the multiple regression models suggest that some factors could be influencing flower abundance patterns. In this case, the high correlation found between the number of plants with flowers and the relative day length suggests, that flower production for a large number of species in this community might be triggered by small changes in day length, even though our study site is not far from the equator.

This variable is known to trigger phenological phases of many temperate plant species (i.e. Heide 1994), but it remains to be experimentally tested whether of not it is important for tropical plants. On potential selective grounds the relationship between flowering at the community level and irradiation (which is highly correlated with the difference in maximum and minimum temperatures), suggest that hot sunny days could be appropriate to open flowers, when pollinator activity and abundance is the greatest. These potential advantages postulated for the plants of this community could be subject to future experiments to test their relevance in pollination processes, particularly in a species-specific basis. Fruit production variation can be associated to temporal changes in pollination efficiency (Burd 1994). Other large-scale processes such as la niña and el niño ENSO, known to influence fruit production at the community level (Wright *et al.* 1999), were not evident in the sampled years, since we have seen a very constant pattern of production.

A proportion of the species from which we recorded leaf phenology (8 out of 24) seasonally lose all their leaves. Four of these species lost their leaves during the dry period and represent a large proportion of deciduous tree species in the community (Stevenson *et al.* 2000b). Terborgh & van Schaik (1987) proposed that the scarcity of folivorous primates in the New World was due to a synchronization in community-wide production patterns of young leaves and fruits, so that there will not be alternative food items such as young leaves in periods of fruit scarcity. However, the new leaves production pattern of the selected species did not show any particular peak of production and it was uncorrelated with fruit production, contrary to the assumption of the hypothesis. In fact, all three ateline primates at Tinigua are able to find young leaves to supplement their diets during periods of fruit scarcity (Stevenson *et al.* 2000a).

Production of fruits with wind, water, and mechanically dispersed seeds was the highest during dry periods, when the trade winds from the northeast are very strong, carrying away the clouds and many seeds. Furthermore, explosive dehiscence is more frequent in dry periods. This production pattern is also consistent to other Neotropical sites (Ibarra-Manriquez *et al.* 1991, Terborgh 1983), in the sense that at least one fruit abundance peak occurs in the dry period. The species that produced fruits during the rainy period are water-dispersed and are frequently found in flooded forests (e.g. *Combretum laxum* Jack. and *Mascagnia ovatifolia* (H.B.K.) Griseb.). The fruit abundance pattern of animal dispersed seeds showed the highest peaks at the beginning of the rainy period, which also occurs in Neotropical lowland forests (Foster 1982, Frankie *et al*. 1974, Justiniano & Fredericksen 2000, Terborgh 1983). However, there is much variation in this pattern across tropical localities (van Schaik & Pfannes in press). For example, homogeneous patterns of fruit production tend to occur in sites with no severe dry season (e.g. Hilty 1980).

Although, it is common that the period of fruit scarcity during the dry season in Neotropical forests, this is not the case at Tinigua, where the greatest density of individuals bearing ripe fleshy fruits occurs about 2.5 months prior to the peak of rains, and the abundance of fleshy fruits during the dry period is higher than at

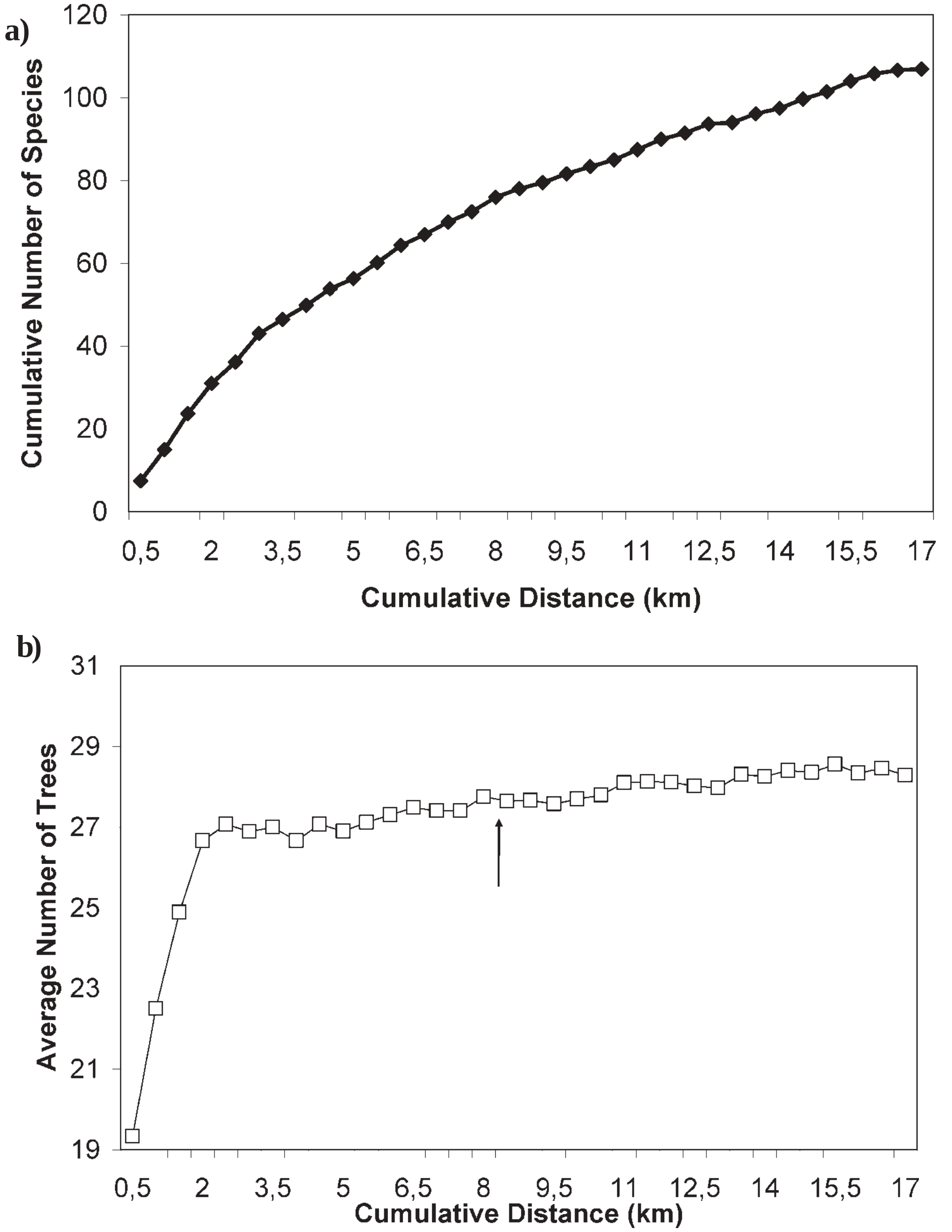

Figure 13. Sampling effort necessary for the stabilization of four different parameters to assess ripe fleshy fruit abundance. Figures show cumulative values estimated during a sampling episode in May 2000 at Tinigua National Park (Colombia), as a function of cumulative transect distance. Each point corresponds to the averages from six simulations in which transect order was set at random. The arrows represent the distance where the estimate remained within the 5% probability respect to the final value a) Number of species, b) Number of trees.km^{-1}, c) Basal area of fruiting trees d) Similarity rank index (see text for details).

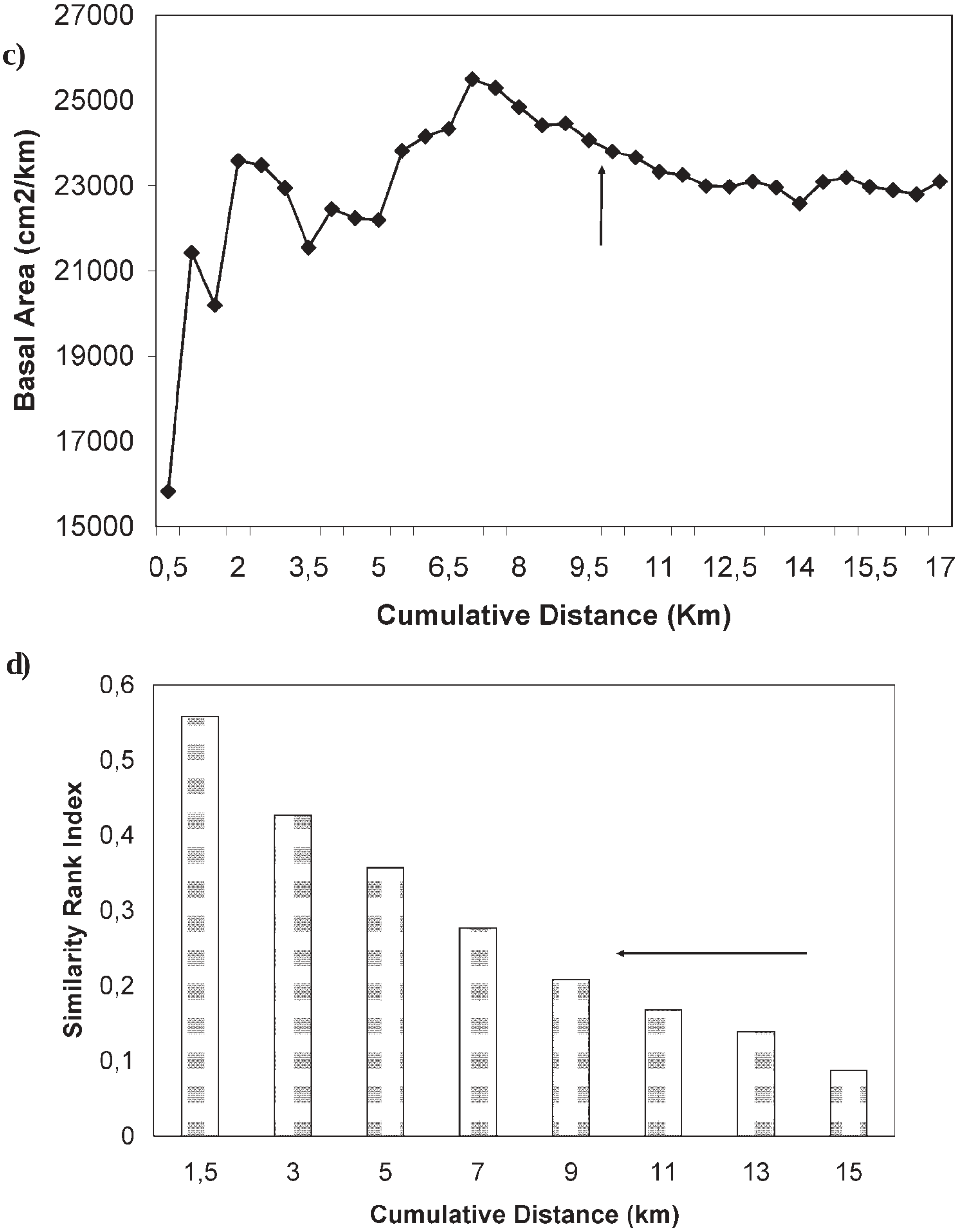

Figure 13 (Cont). Sampling effort necessary for the stabilization of four different parameters to assess ripe fleshy fruit abundance. Figures show cumulative values estimated during a sampling episode in May 2000 at Tinigua National Park (Colombia), as a function of cumulative transect distance. Each point corresponds to the averages from six simulations in which transect order was set at random. The arrows represent the distance where the estimate remained within the 5% probability respect to the final value a) Number of species, b) Number of trees.km^{-1}, c) Basal area of fruiting trees d) Similarity rank index (see text for details).

the end of the rainy season. The adaptive significance of this pattern has been addressed by several theories (Garwood 1982, van Schaik *et al.* 1993), and some of them are consistent with our findings at Tinigua Garwood (1982) showed that the production of seeds at the beginning of the rainy period allows the germinated seedling to experience less water stress during the critical first few months of development. Seed predation experiments in the area suggest that in many cases seed survival could be greater under high seed density treatments, probably due to predator satiation (Stevenson 2002). Also we might expect to find lower predation rates during periods of high fruit and seed production (van Schaik *et al.* 1993). Thus, a peak of fruit production should reduce seed predation risk, while the timing of this peak just prior or at the beginning of the rainy season would assure good water supplies during the critical period of seedling establishment. In any case, it would be important to carry out more experimental studies to test these potential advantages.

Methodological Considerations

We have discussed previously pros and cons of different methods to assess fruit abundance (Stevenson *et al.* 1998), and the main points are summarized below.

1. Fruit traps estimates are sensitive to trap location biases and chance effects. For example the high fruit production peak in October (see Fig 8) was caused by a single frugivory bout by a capuchin monkey who dropped palm fruits just above a trap. Therefore, this unlikely event seems to indicate a period of high fruit abundance during the fruit scarcity period. However, it represents the chance of placing a trap just underneath a clumped resource that was available in the scarcity period. This kind of problem can be corrected by redistributing fruit weight homogeneously during the fruiting time of that species (Janson 1984).

2. The basal area approach may overestimate production of large trees that do not always bear large crops. For example, fruit production of a single large fig tree (DBH about 1.5m) in the flooded forest was responsible for the peaks in June-July and again in January (Fig. 8). Although, during June-July the tree dropped 17.3 g of fruit into three traps, during the second fruiting episode it dropped only 5.6 g in. In the first episode fruit production was at least three times greater, but the basal area estimate did not show that pattern. Moreover, as the second fruit crop was so small and short, all the basal area was assigned to a single phenology sample, skyrocketing the production in that period, in contrast to the first episode when the basal area was divided into two biweekly revisions. Another source of bias when using basal area estimates is the subestimation in the production of palms. Because of its particular architecture and growth form we should not expect a positive linear relation between basal area and fruit production.

3. The number of fruiting trees usually shows a gradual change of the fruit production pattern, without any of the unrealistic peaks discussed above. However, it is inappropriate to use the number of fruiting trees as a fruit production estimator in species-specific analyses, because production of dense but small trees might be overestimated, while production of large trees underestimated (see for example the importance of small cacao trees in Table 3).

The new methodology proposed in this study avoids all the problems that I just discussed. Therefore I highly recommend it, if species-specific fruit abundance patterns must be quantified (for general community patterns other less demanding methods, such as the number of individuals in transects, yield similar results).

My impression is that the new method proposed was as time-consuming as the fruit traps (based on the fact that I had morphological measures for a variety of plant species before the analysis, and that I assumed that the small sample size for the estimates did not alter the final results). Additional observations will be necessary to test these assumptions. Perhaps the weakest step in the calculations to estimate fruit production using the new methods was the inaccuracy of the visual method to assess fruit production of individual plants. This variable is known to be very difficult to measure in the field (Chapman *et al.* 1992), and we could find a good relationship between visual estimates and fruit production from fruit traps to correct the data. The feasibility of using the method depends on an accurate method to correct the visual estimates of fruit abundance. I encourage future researchers to use and refine this kind of visual approach, because this study proved that better estimates might be gathered from the visual estimates than from commonly recommended methods such as basal area, DBH, or crown area (Chapman *et al.* 1992). In the worst case the visual estimates could be used as ranks, which are commonly used in phenological studies, while the reverse transformation is impossible.

Although at the moment I do not have any independent way to prove that the new method was free from biases, based on my experience using a variety of methods to measure fruit production, this new method showed less discrepancies with the observed patterns. My only doubt so far refers to the inclusion of so many palm species in the list of the most productive species (Table 3). It is possible that the visual assessment of palm production was intermediate between cauliflorous species and plants bearing fruits in the crown, because the visibility of the fruits is blocked by other fruits and inflorescence branches, but not by leaves or twigs as in common trees. In absence of a correcting factor of visual estimates for any palm species I used the same correcting factor as the one used for common tree species. This can be related to their great contribution to fruit abundance, however, it is difficult to be certain that the results are biased, because palm fruits are heavy, and the fruit trap methods in other years also have shown that the most productive species in the area are the palms (Stevenson *et al.* 1998). Also, this is supported by other studies which have found that palm species are known to be abundant and to play important ecological roles in many Neotropical communities (Peres 1994a, Stevenson *et al.* 2000a, Terborgh 1983). A recommendation for future studies is to include of palm species for comparative analyses between visual and fruit trap estimates.

Finally, if economic or time constraints make impossible to undertake a phenological study of this kind, and just a general assessment of community wide fruit production is required, I suggest to use the number of fruiting individuals in phenological transects as a proxy. This variable provided community wide estimates that are well correlated with other more meticulous methods, and it is easy to measure (Stevenson *et al.* 1998, fig. 10). Also it stabilizes with relatively low sampling effort (fig 13 b). However, this measure, unlike the new method, will not be easy to compare across studies in different communities (Janson & Chapman 1999). For example, the number of trees located in transects of a certain length will not be comparable among localities when the average production of plants differs or when visibility varies among sites. In contrast, the new methodology offers estimates of km/ha which are comparable with all methods measuring fruit production in standard units.

Sampling Effort in Phenological Transects

The sampling effort needed to assess community-wide fruit production using phenological transects will vary depending on the fruit abundance estimate used and the question to be answered. For instance, much more effort would be needed to know the total number of plant species producing fruits than the number of trees producing fruit in the transects (>17 km. vs. 8 km. respectively). According to our results, the sampling distance necessary to quantify fruit abundance using basal area in the community should be at least 10 km, while 8 km are needed to have a stable ranking of the most important species. All these values are approximations to the sampling distance required to quantify fruit abundance in the non-flooded forests at Tinigua National Park. Therefore these minimum estimates could change for other forest types, other localities, and seasons. I suggest undertaking similar intensive surveys and analyses prior to start phenological studies, in order to set adequate sampling procedures in a given locality. However, in absence of such information I hope that this study provides some guidelines for the effort needed to achieve different levels of detail in phenological studies using transects.

ACKNOWLEDGEMENTS

I would like to thank all the colleagues and field assistants who helped in gathering information, especially to Marcela J. Quiñones, Jorge A. Ahumada, María C. Castellanos, Alicia Medina, Carolina García, Andrés Link, Alejandro Franco, Mabel Suescún, Tatiana Samper, and Mónica Pineda. I thank Charles Janson, Patricia Wright, and John Fleagle for their comments. This study was possible thanks to the help of different institutions such as La Fundación para la Promoción de la Investigación y la Tecnología (Banco de la República), Margot Marsh Foundation, Lincoln Park Zoo, Primate Conservation Inc., IdeaWild, Colciencias, and CIEM.

LITERATURE CITED

AUGSPURGER, C. 1982. A cue for synchronous flowering. pp 133-155. In Leigh, E.G., A. S. Rand & D. M. Windsor, (eds.). The ecology of a neotropical forest: Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington D.C.

BLAKE, J. G., B. A. LOISELLE, T. C. MOERMOND, D. J. LEVEY & J. S. DENSLOW. 1990. Quantifying abundance of fruits for birds in tropical habitats. Studies in Avian Biology 13: 71-77.

BOTERO, P. 1998. Paisajes fisiográficos de la Orinoquia-Amazonia (ORAM), Colombia. Análisis Geográficos 27-28: 1-317.

BURD. 1994. Bateman principle and plant reproduction - the role of pollen limitation in fruit and seed set. Botanical Review 60: 83-139.

BURNHAM, K. P., D. R. ANDERSON & J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs No.72: 7-202.

CHAPMAN, C. A., L. J. CHAPMAN, K. WRANGHAM, D. GEBO & L. GARDNER. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24: 527-531.

CHAPMAN, C. A., R. WRANGHAM & L. J. CHAPMAN. 1994. Indexes of habitat-wide fruit abundance in tropical forests. Biotropica 26: 160-171.

CORLETT, R. T. & J. V. LAFRANKIE. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. Climatic Change 39: 439-453.

CROAT, T. B. 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). Biotropica 7: 270-277.

CURRAN, L. M. & M. LEIGHTON. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. Ecological Monographs 70: 101-128.

DAUBENMIRE, R. 1971. Phenology and other characteristics of tropical semi-deciduous forests in North-western Costa Rica. Journal of Ecology 60: 147-170.

FOSTER, R. B. 1982. The seasonal rhythm in fruitfall on Barro Colorado Island. pp. 151-172. In: E. G. J. Leigh, A. S. Rand & D. M. Windsor, (eds.). The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington, DC.

FRANKIE, G. W., H. W. BAKER & P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dey forsts in the lowlands of Costa Rica. Journal. Journal of Ecology 62: 881-919.

FUENTES, M. 1992. Latitudinal and elevational variation in fruiting phenology among western-european bird-dispersed plants. Ecography 15: 177-183.

GARWOOD, N. 1982. Seasonal rythm of seed germitation in a semideciduous forest. pp. 173-185. In: E. G. J. Leigh, A. S. Rand, and D. M. Windsor, eds. The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington, DC.

HEIDE, O. M. 1994. Control of flowering and reproduction in temperate grasses. New Phytologist 128: 347-362.

HEMINGWAY, C. A. & D. J. OVERDORFF. 1999. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. Biotropica 31: 354-364.

HERRERA, C. M. 1998. Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal. The American Naturalist 152: 576-594.

HILL, D. A. & N. AGETSUMA. 1995. Supra-annual variation in the influence of *Myrica rubra* fruit on the behavior of a troop of japanese macaques in Yakushima. American Journal of Primatology 35: 241-250.

HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. Biotropica 12: 292-306.

HIRABUKI, Y. 1990. Vegetation and landform structure in the study area of La Macarena: A physiognomic investigation. Field Studies of New World Monkeys, La Macarena, Colombia 3: 35-48.

HUBBELL, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. Oikos 35: 214-229.

IBARRA-MANRÍQUEZ, G., B. SÁNCHEZ-GARFIAS & L. GONZÁLEZ-GARCÍA. 1991. Phenology of anemochorous vines and trees in a Mexican tropical rain-forest. Biotropica 23: 242-254.

JANSON, C. H. 1984. Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). *Z. Tierpsychol.* 65: 177-200.

JANSON, C. H. & C. A. CHAPMAN. 1999. Resources and primate community structure. pp. 237-267. In: J. G. Fleagle, C.H. Janson & K. Reed (eds.). Primate Communities. Cambridge University Press, Cambridge; New York.

JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Costa Rica. Evolution 21: 620-637.

JUSTINIANO, M. J. & T. S. FREDERICKSEN. 2000. Phenology of tree species in Bolivian dry forests. Biotropica 32: 276-281.

KAPLIN, B. A., V. MUNYALIGOGA & T. C. MOERMOND. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). Biotropica 30: 56-71.

KNOTT, C. D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. International Journal of Primatology 19: 1061-1079.

KOENIG, A. 1997. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). Journal of Zoology 243: 215-235.

KOLLMANN, J. & D. GOETZE. 1998. Notes on seed traps in terrestrial plant communities. Flora 193: 31-40.

LEIGHTON, M. & D. R. LEIGHTON. 1982. The relationship of size of feeding aggregate to size of food patch - howler monkeys

(*Alouatta palliata*) feeding in *Trichilia cipo* fruit-trees on Barro Colorado Island. Biotropica 14: 81-90.

Loiselle, B. A. & J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80: 330-336.

Mandujano, S. 1999. Variation in herd size of collared peccaries in a Mexican tropical forest. Southwestern Naturalist 44: 199-204.

Newstrom, L. E., G. W. Frankie & H. G. Baker. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain-forest trees at La-Selva, Costa-Rica. Biotropica 26: 141-159.

Overdorff, D. J. 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. International Journal of Primatology 14: 721-753.

Peres, C. A. 1994a. Composition, density, and fruiting phenology of arborescent palms in an Amazonian terra-firme forest. Biotropica 26: 285-294.

Peres, C. A. 1994b. Primate responses to phenological changes in an Amazonian terra-firme forest. Biotropica 26: 98-112.

Renton, K. 2001. Lilac-crowned parrot diet and food resource availability: Resource tracking by a parrot seed predator. Condor 103: 62-69.

Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A. A. Hamid & T. Nakashizuka. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. American Journal of Botany 86: 1414-1436.

Stevenson, P. R. 2002. Frugivory and seed dispersal by woolly monekys (Lagothrix lagothricha) at Tinigua Park, Colomiba. Ph.D. dissertation. SUNY at Stony Brook, New York.

Stevenson, P. R., M. C. Castellanos & M. P. Medina. 1999. Elementos arbóreos de los bosques de un plano inundable en el Parque Nacional Natural Tinigua, Colombia. Caldasia 21: 38-49.

Stevenson, P. R., M. J. Quiñones & J. A. Ahumada. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at La Macarena, Colombia. American Journal of Primatology 32: 123-140.

Stevenson, P. R., M. J. Quiñones & J. A. Ahumada. 1998. Annual variation if fruiting pattern using two different methods in a lowland tropical forest at Tinigua National Park, Colombia. Biotropica 30: 129-134.

Stevenson, P. R., M. J. Quiñones & J. A. Ahumada. 2000a. Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. Biotropica 32: 533-544.

Stevenson, P. R., M. J. Quiñones & M. C. Castellanos. 2000b. *Guía de Frutos de los Bosques del Río Duda, La Macarena, Colombia*. Asociación para La Defensa de La Macarena - IUCN, Santafé de Bogotá.

Terborgh, J. 1983. Five New World Primates. A study on comparative ecology. Princeton University Press, Princeton.

Terborgh, J. & C. P. Van Schaik. 1987. Convergence vs. nonconvergence in primate communities. pp. 205-226. In: J. H. R. Gee & P. S. Giller, (eds.). Organization of Communities, Past and Present. Blackwell Scientific Publications, Oxford.

Tutin, C. E. G., R. M. Ham, L. J. T. White & M. J. S. Harrison. 1997. The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology 42: 1-24.

Van Dulmen, A. 2001. Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. Plant Ecology 153: 73-85.

Van Schaik, C. P. & K. Pfannes. 2003. Tropical climates and phenology: a primate perspective. (in press).

Van Schaik, C. P., J. W. Terborgh & S. J. Wright. 1993. The phenology of tropical forests - adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24: 353-377.

Viana, B. F., A. D. P. Kleinert & V. L. Imperatriz-Fonseca. 1997. Abundance and flower visits of bees in a cerrado of Bahia, tropical Brazil. Studies on Neotropical Fauna and Environment 32: 212-219.

Wich, S. A. & C. P. Van Schaik. 2000. The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malasia. Journal of Tropical Ecology 16: 563-577.

Wrangham, R. W., N. L. Conklin-Brittain & K. D. Hunt. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. International Journal of Primatology 19: 949-970.

Wright, S. J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72: 1643-1657.

Wright, S. J. 1994. Light and the phenology of tropical trees. American Naturalist 143: 192-199.

Wright, S. J. 1995. Phylogenetic patterns among tropical flowering phenologies. Journal of Ecology 83: 937-948.

Wright, S. J., C. Carrasco, O. Calderon & S. Paton. 1999. The El Nino Southern Oscillation variable fruit production, and famine in a tropical forest. Ecology 80: 1632-1647.

Zhang, S. Y. & L. X. Wang. 1995. Comparison of three fruit census methods in French-Guiana. Journal of Tropical Ecology 11: 281-294.

Recibido: 30/09/2003
Aceptado: 03/02/2004